HOKKAIDO UNIVERSITY

Title	TWO NEW PARLATORIINE SCALE INSECTS WITH ODONASPIDINE CHARACTERS : THE OTHER SIDE OF THE COIN (HOMOPTERA : COCCOIDEA : DIASPIDIDAE)
Author(s)	TAKAGI, Sadao
Citation	Insecta matsumurana. Series entomology. New series, 37: 1-25
Issue Date	1987-10
Doc URL	http://hdl.handle.net/2115/9839
Right	
Type	bulletin
Additional Information	

Instructions for use

TWO NEW PARLATORIINE SCALE INSECTS WITH
ODONASPIDINE CHARACTERS :
THE OTHER SIDE OF THE COIN
(HOMOPTERA : COCCOIDEA : DIASPIDIDAE)

By SADAO TAKAGI

Research Trips for Agricultural and Forest Insects in the Subcontinent of India [Grants-in-Aid for Overseas Scientific Survey, Ministry of Education, Japanese Government, 1978, No. 304108 ; 1979, No. 404307 ; 1983, No. 58041001 ; 1984, No. 59043001], Scientific Report No. 26.

Scientific Results of the Hokkaidô University Expeditions to the Himalaya.

Abstract

TAKAGI, S. 1987.   Two new parlatoriine scale insects with odonaspidine characters : the other side of the coin (Homoptera : Coccoidea : Diaspididae).   *Ins. matsum. n. s.* 37 : 1-25, 13 figs. (13 pls.).

Two species of the Parlatoriini, *Neparla katus*, n.g., n. sp., and *Tamilparla smilacis*, n.g., n. sp., are described from Nepal and South India, respectively.   The females occur under the stipules of the host plants (*Castanopsis indica* and *Smilax* sp., respectively).   In both species the exuviation of the second instar female is of the bivalve type as in the Odonaspidini.   The adult females also approach the Odonaspidini in some characters.   This, coupled with the second instar polymorphism in the Odonaspidini and *Smilacicola* (which may represent the Rugaspidiotini), illustrates the potential in the genome of the Parlatoriini and their ancestor for the manifestation of odonaspidine characters, and, consequently, the possible polyphyletic origin of the Odonaspidini.

Author's address. Entomological Institute, Faculty of Agriculture, Hokkaidô University, Sapporo, 060 Japan.

Contents. Neparla katus, n.g., n. sp. — *Tamilparla smilacis*, n.g., n. sp. — Higher taxa within the Diaspididae — The Rugaspidiotini and the Odonaspidini — The other side of the coin — Parallel evolution.

In the course of my study on the scale insect material which I collected in Nepal and India I have found two species of the Parlatoriini occurring under the stipules of their host plants. They are unusual for parlatoriines because the exuviation of their second instar females is of the bivalve type as in the tribe Odonaspidini. They also approach the Odonaspidini in some characters of the adult female. Coupled with the fact that the Odonaspidini manifest an unmistakable parlatoriine pattern in the characters of the second instar male, these species strongly suggest an aspect essential to organismal evolution.

Before going further, I express my gratitude to Prof. James O. Howell, University of Georgia, for his reading through the manuscript and for his suggestions for improvement of the manuscript.

DESCRIPTION

Neparla, n.g.

Nominifer [type-species] : *Neparla katus*, n. sp.

Apparently close to *Parlatoria*, but disagrees with the latter mainly in the following characters.

In the adult female :

1) Pygidial macroducts occur on the ventral surface as well.

2) The perivulvar disk pores are arranged in an arch (which may be incomplete medially).

3) The plates are rudimentary laterally to the third lobes.

In the second instar female :

4) The exuviation is of the bivalve type.

Neparla katus, n. sp.

Material. Collected in Nepal : at Kaski, Pokhara, Gandaki Zone, alt. 800 m, Dec. 1983 ; at Godavari, near Kathmandu, alt. 1600 m, Aug. 1975 ; at Phidim, Mechi Zone, alt. 1350 m, Nov. 1983. On *Castanopsis indica* [Fagaceae ; local name : Dhale Katus].

Nominifer [holotype] : adult female, from Godavari, deposited in the collection of the Entomological Institute, Hokkaidô University.

Observed females occur on the inner side of the stipule, and males on the twig. Scale of female oval, depressed, and white ; entirely enclosing the insect body, ventral portion being as well developed as dorsal ; exuvial casts terminal ; 2nd instar cast (Fig. 7) ruptured along the margin, but not completely, dorsal and ventral halves of skin remaining attached to each other by part of the margin, the ventral half less sclerotized, its central area including mouth-parts pushed back toward pygidium ; 1st instar cast ruptured on the ventral surface of the head, retaining antennae, the rest of ventral skin much less sclerotized and eventually completely separated from dorsal skin, together with legs and mouth-parts pushed backward. Scale of male much smaller, slender, with sides straight and parallel ; pale brown dorsally and white ventrally.

Adult female [based on 10 specimens from Kaski, 15 from Godavari, and 15 from Phidim] (Figs. 1-3). Body broadly obovate ; meso- and metathorax and abd I-IV well defined marginally by intersegmental constrictions ; pygidium triangular

rather than round on the free margin. Anus situated at about basal 1/3 of pygidium, surrounded by a thickly sclerotized patch of derm. Prepygidial derm remaining membraneous.

Three pairs of well-developed pygidial lobes, presenting a converging appearance apically toward meson; Lls largest, separated from each other by a space nearly 1/3 as wide as one of them, L2 and L3 progressively smaller; as broad as or a little broader than long, usually deeply notched once on the outer side. L4 represented by a low, sclerotized, pointed process or merged into pygidial margin. Two plates between Lls, 2 between L1 and L2, and 3 between L2 and L3, all these plates well represented, little extending beyond the apices of the lobes, slender, spiniform or only a little fimbriate; outside L3 the plates are rudimentary and spiniform, 4 or 5 plates are recognized between L3 and L4, and some inconspicuous ones are discernible outside L4. Gland tubercles well represented, 0-6 in the prespiracular group, 2-17 in the anterior spiracular, 5-26 in the mesothoracic and 3-26 in the metathoracic.

Submedian dorsal macroducts present, forming 3 clusters on each side as follows: 4-16 on abd VII laterally to anus, 5 to nearly 20 on abd VI [when numerous, these macroducts may be confluent with submarginal macroducts and cannot be exactly counted], and 4-18 on abd V. Marginal and submarginal dorsal macroducts of pygidium larger than the submedian macroducts, their orifices nearly as broad as, though some of them narrower than, anus, marginal macroducts with an unusually thickened rim around the orifice; 1 marginal macroduct always present between Lls, and 1 between L1 and L2; some 20-30 macroducts occurring in marginal to submarginal zone between L2 and lateral end of pygidium, their arrangement suggesting segmental rows belonging to abd V-VII, the row supposedly belonging to abd VI often extending anteriorly and sometimes confluent with the submedian cluster of the segment, the macroducts in the extended row usually reduced in size, becoming almost as large as the submedian macroducts. Ventral macroducts present on abd V and VI near margin, as large as the dorsal macroducts, about 6-12 in total on one side. Numerous macroducts occurring in a broad submarginal zone on dorsal and ventral surfaces of prepygidial segments as anteriorly as mesothorax, reducing in size anteriorly, thus merging into microducts.

Ventral surface spiculate in a broad median area along posterior margins of prepygidial segments and also laterally to mentum. Ventral microducts rather abundant, mingled with the spicules in prepygidial region. Anterior spiracle accompanied with a loose cluster of 3-13 5-locular disk pores; posterior spiracle without disk pores. Perivulvar disk pores forming a pair of longitudinal clusters laterally to vulva, which are connected by their anterior ends through a single or partly or completely double transverse row, this row sometimes incomplete or rarely lacking; 57-119 disk pores in total. Dorsal intersegmental suture between abd V and VI strongly sclerotized submarginally for a short distance, forming an apparently folded-in pocket-like structure. A small "crack" of derm present between posterior spiracle and body margin [where the "derm pocket" is expected in *Parlatoria*]. Antenna a low tubercle with small spinous processes and a short curved seta.

Second instar female [based on 5 specimens from Godavari and 5 from Phidim] (Fig. 4). Body round; pygidium broadly triangular on free margin. Anus situated about centre of pygidium. Pygidial lobes nearly as in adult female, but Lls set close

3

together.   Plates spiniform, 2 between L1s, 2 between L1 and L2, and 2 between L2 and L3 ; some plates occurring sparsely as anteriorly as abd II, mostly rudimentary. Gland tubercles rudimentary, 1 prespiracular and 1 anterior spiracular.   Marginal macroducts : 1 between L1 and L2, 1 between L2 and L3, 2 between L3 and L4 ; 3-5 on abd I-V (usually absent on abd I).   Submarginal macroducts : 1 on each of abd I (or II)-VI.   Submedian macroducts present or absent, when present much smaller, occurring on abd V-VII or only on VI or VII, 1 on V and VII and 1 or 2 on VI. Anterior spiracle with 2-4 disk pores.   Antenna a low tubercle, with small spinous processes and a short seta.   Ventral derm roughly scaly in a broad mediobasal area of pygidium ; spinulose in a broad median area along posterior margins of pre-pygidial segments and also laterally to mentum.

Second instar male [based on 5 specimens from Godavari and 5 from Phidim] (Fig. 5).   Differs from the 2nd instar female in having much more numerous submarginal macroducts, which extend anteriorly up to the thoracic region, where they occur on both surfaces.   Submedian dorsal macroducts always present, as large as submarginal macroducts, 2-4 on abd V and also VI, 2-3 on VII.   Gland tubercles well represented, 1-5 in the prespiracular group, 2-5 in the anterior spiracular, 2-7 in the mesothoracic, 1-6 in the metathoracic, and 1-3 (rarely 0) in the 1st abdominal.

First instar larva (Fig. 6).   Head without enlarged dorsal ducts.   Antenna short, 5-segmented ; segm III apparently longer than II and IV, segm V nearly as long as II-IV combined, annulate.

Tamilparla, n.g.
Nominifer [type-species] : *Tamilparla smilacis*, n. sp.
Related to *Parlatoria*, but distinguishable from the latter mainly by the following characters.
In the adult female :
1)   Numerous macroducts, comparatively small in size, occur all over the dorsal surface of the pygidium except on the median basal area anterior to the anus.
2)   Some marginal macroducts with an associated thick sclerosis superimposed on the rim of the orifice.
In the second instar female :
3)   The exuviation is of the bivalve type.
Thick scleroses associated with marginal macroducts of the pygidium also occur in *Parlatoreopsis*, which, however, shows no close relation to the new genus in other respects.   *Kandraspis*, proposed for the Madagascan *K. euphorbiae*, may be a parlatoriine, having two-barred ducts and undivided lateral lobes, and is characterized by "abundant small ducts scattered over the pygidium".   As described and illustrated by Mamet (1959) this scale insect does not appear to have any close relation to the new genus.   His illustration shows that the dorsal ducts do not occur over the whole pygidium but are confined to a broad marginal to submarginal zone. Further, it seems from his description that his species lives exposed on the stem of the host plant.

Tamilparla smilacis, n. sp.
Material.   Collected in Bharat [India] : at Coonoor, Nilgiri, Tamil Nadu, alt. ca. 1800 m, Nov. 1978.   On *Smilax* sp. ("near *S. wrightii*" according to identification

by the Botanical Survey of India, Coimbatore) [Liliaceae].

Nominifer [holotype] : adult female, deposited in the collection of the Zoological Survey of India.

Both males and females concealed under the stipule. Scale of female oval, pale brown dorsally, the ventral portion developed only on the sides, forming a trough-shaped cavity inside the scale ; exuvial casts terminal ; 2nd instar cast (Fig. 10) reddish brown, blackish medially, the ventral skin ruptured along margin but remaining attached to dorsal skin by anterior margin, less sclerotized than the dorsal skin, its central area being pushed backward together with mouth-parts. Male scale much smaller, elongate, pale brown dorsally.

Adult female [based on 15 specimens] (Figs. 8-11). Body broadly obovate ; meso- and metathorax and abd I-IV defined marginally by intersegmental constrictions, the constriction separating the mesothorax from the prothorax often appearing deeper, giving the united head and prothorax an appearance of being set off from the rest of the body ; pygidium broadly rounded along the free margin. Anus situated near centre of pygidium, surrounded by a thickly sclerotized patch of derm. Derm remaining membraneous except for dorsum of pygidium and prepygidial body margin up to mesothorax ; reticulate around anus.

Pygidial lobes in 4 pairs ; Lls separated from each other by a space as wide as or narrower than one of them, as long as or shorter than broad, flatly and broadly round apically ; lateral lobes successively shorter, often irregularly notched, L4 represented by a low, broad prominence. Plates well represented on pygidium ; 2 between Lls and 2 between L1 and L2 slender, more or less fimbriate on sides ; 3-4 between L2 and L3, 3-5 between L3 and L4, these plates somewhat variable in shape, but generally broader and more or less fimbriate ; 4-6 plates outside L4, usually broad basally and narrowing apically. Similar plates occurring on prepygidial segments up to posterior angle of abd I, becoming little fimbriate. Gland tubercles well represented on prothoracic area, sclerotized, 9-22 in number on one side, forming a transverse cluster within the posterolateral corner of the fused head and prothorax : no gland tubercles on other segments.

Dorsal macroducts rather small, their orifices much smaller than anus ; numerous ones, over 70 to ca. 130 on one side, are strewn over the pygidium except mediobasally (anteriorly to the anus). Prepygidial dorsal macroducts also numerous, extending submarginally as far as mesothorax. Ventral macroducts abundant in lateral lobes of meso- and metathorax. Dorsal macroducts occurring along pygidial margin very thickly rimmed on the orifice ; 1 or 2 between Lls, the orifice(s) enclosed between a pair of small scleroses arising from inner basal angles of Lls ; 1 or 2 between L1 and L2, with a robust sclerosis superimposed on the mesal side of the rim (of the mesal macroduct when there are 2) ; 2-4 between L2 and L3, the outermost one (situated just mesad of L3) with a robust sclerosis superimposed on the mesal side of the rim ; 4-6 between L3 and L4, the outermost usually with a sclerosis on the mesal side of the rim ; 2-5 outside L4.

Microducts abundant around anterior spiracle. Anterior spiracle with a loose cluster of 2-8 5-locular disk pores ; posterior spiracle without disk pores. Perivulvar disk pores in 5 groups, the median group often reduced to a few scattered disk pores ; 3-9 in the median group, 19-32 in the anterolateral, and 24-37 in the posterolateral. Antenna a flat tubercle with some short spines and a short curved

seta. Eye modified into a sclerotized robust spine. Derm minutely spiculose later-
ally to mentum.

Second instar female [based on 9 specimens] (Fig. 12). Body obovate;
pygidium roundish along the free margin. Anus situated near centre of pygidium.
Lls separated from each other by a space nearly as wide as one of them, longer than
broad, deeply notched once subapically on the outer margin, broadly rounded on the
apical margin. L2 and L3 similar in shape to but a little smaller than L1 ; L4 a low,
angular, sclerotized process, serrate on its slanting outer margin. Processes which
may represent rudimentary lobes (L5-L8) discernible up to abd I, membraneous,
more or less similar in shape to adjacent plates, but lacking a microduct running
through. Plates well represented ; 2 between Lls and 2 between L1 and L2 slender,
little or slightly fimbriate ; 3 between L2 and L3 broader, tending to be fimbriate on
the sides ; 3 between L3 and L4 more developed ; 2 laterally to L4 on abd V, broad,
fimbriate on the slanting outer margin ; 3 on abd IV, one of them being situated
posteriorly and the other two anteriorly to L5, broad, fimbriate on the slanting outer
margin ; abd II and III likewise each with 3 plates ; abd I with 1 plate at poster-
olateral angle. Gland tubercles absent. Marginal macroducts : 1 between L1 and
L2, 2 between L2 and L3, 2 between L3 and L4, 1 laterally to L4 on abd V ; 2 on each
of abd II-IV, and 1 in posterolateral angle of abd I. Macroducts situated just
mesally to L1, L2 and L3 with rim of orifice thickened on mesal side ; a small
cordiform sclerosis present between bases of Lls. Submarginal dorsal macroducts
3-9 on one side of body, occurring on abd II-VII when distributed most extensively,
usually 1 or 2 on one segment (1-3 on abd VI). Ventral microducts rather numerous
on prothorax. Anterior spiracle with 2 or 3 5-locular disk pores. Antenna a low
tubercle with small spinous processes and a short seta. Ventral derm scaly in a
broad mediobasal area of pygidium ; minutely spiculose laterally to mentum.

Second instar male [based on 8 specimens] (Fig. 13). Differs from the 2nd
instar female in having gland tubercles, submedian dorsal macroducts, and more
numerous submarginal macroducts. Submedian macroducts usually occurring on
abd IV-VII, 1 or 2 (always 1 on abd VII) on one segment. Submarginal dorsal
macroducts occurring as anteriorly as mesothorax, submarginal ventral macroducts
on thoracic segments. Gland tubercles 1-3 in the prespiracular group, 1-5 in the
anterior spiracular, 1-3 in the mesothoracic, 1-3 in the metathoracic, and 1-2 in the
1st abdominal. Anterior spiracle with 1-4 disk pores.

First instar larva (Fig. 12). Head without enlarged dorsal ducts. Antenna
5-segmented, segm III a little longer than II and IV ; segm V as long as segm I-IV
combined, annulate.

DISCUSSION

Higher taxa within the Diaspididae
The great majority of diaspidids are provided with marginal appendages in the
adult female and the larval stage. There are two principal patterns for these
appendages : one is characterized by a combination of lobes and plates with the
lobes all undivided, whereas the other pattern shows a combination of lobes and
gland spines instead of plates, with the lobes bilobulate, except for the median lobes.
These patterns are not always distinct probably owing to secondary modifications.

These appendages may be rudimentary or completely lost in the adult female, but may still be present in the larval stage. Some forms appear to be primarily without lobes or any appendages, and may be relics of the primitive stock of the family.

On the basis of these patterns most of the diaspidids having appendages are divisible into two groups, which may be treated as subfamilies: the Aspidiotinae having plates and undivided lobes and the Diaspidinae having gland spines and bilobulate lobes. They may be divided into subgroups or tribes as follows:

Aspidiotinae
Leucaspidini
Parlatoriini
Rugaspidiotini [as represented by *Smilacicola*]
Odonaspidini
Aspidiotini
Diaspidinae
Lepidosaphedini
Diaspidini

The Rugaspidiotini and the Odonaspidini are referred to the Aspidiotinae on the basis of larval characters. Although larvae of only a limited number of species of these tribes are known, they clearly show lobes and plates.

The Rugaspidiotini and the Odonaspidini

The name Rugaspidiotini is based on the North American *Rugaspidiotus arizonicus*. This species, however, is rather isolated, finding no particularly close relatives (Ferris 1938). In the first instar it has some characters common to *Odonaspis secreta*, the nominifer of *Odonaspis*, though differing in lacking distinct lobes (Howell et al. 1986). No detailed study has been made on the second instar of *R. arizonicus*, and little on the larval stage of any other North American species referred to the Rugaspidiotini. This tribe is here understood as represented by the Asian genus *Smilacicola*, of which the larval stage is well known (Takagi 1983). However, the possibility is not excluded that this genus is not so closely related to other forms referred to the Rugaspidiotini (Takagi 1983).

The Rugaspidiotini and the Odonaspidini are commonly characterized as follows.

In the adult female:

1) The marginal appendages (lobes and plates) are completely lacking, or the lobes are indicated by low prominences.

2) Abundant ducts are strewn over the pygidium on both surfaces.

In the second instar:

3) Polymorphism occurs, and some forms agree with parlatoriines in the pattern of characters [except for the antennae of the Rugaspidiotini: character (6) below].

4) The exuviation is of the bivalve type, occurring by the splitting of the derm around the margin. The dorsal and ventral halves of the exuvial cast remain attached to each other by part of the margin, the dorsal half becoming incorporated in the dorsal portion of the scale and the ventral half in the ventral portion, which is as well developed as the dorsal.

In the first instar :

5) The lobes are in one pair.

The Rugaspidiotini and the Odonaspidini differ from each other as follows.

6) The antennae of the adult female and the second instar bear more than one seta in the Rugaspidiotini (six setae in *Smilacicola*) and a single seta in the Odonaspidini.

7) The ducts of the adult female are more or less reduced in size in the Odonaspidini.

8) The pygidium of the adult female is usually with marginal scleroses bordering intersegmental furrows in the Odonaspidini.

9) Perivulvar disk pores are present or absent and if present arranged in a more or less continuous arch in the Odonaspidini, while absent in the Rugaspidiotini. (In *Natalaspis*, which may be referred to the Rugaspidiotini, perivulvar pores are present and arranged in five groups as usual with diaspidids.)

10) The antennae of the first instar are five-segmented, the third segment is obviously longer than either the second and the fourth, and the fifth segment is elongate and annulate, in the Odonaspidini.   Shaped otherwise in the Rugaspidiotini.

11) A distinct tibiotarsal joint occurs on the legs of the first instar in the Rugaspidiotini but is absent in the Odonaspidini.

In some characters, especially characters 6), 7) and 11) the Rugaspidiotini are more primitive than the Odonaspidini.   The parlatoriine-patterned second instar suggests that the ancestral forms of these tribes were like the Parlatoriini.   On the other hand, in characters 6) and 11) the Rugaspidiotini are more primitive than the existing Parlatoriini.   All this leads to the following alternative schemes of phylogenetic relationship among these tribes.

(a) $O \longleftarrow R \longleftarrow AP \longrightarrow P$

(b) $R \longleftarrow AP \longrightarrow P \longrightarrow O$

(AP : putative ancestor of the Parlatoriini ; P : the Parlatoriini ; R : the Rugaspidiotini ; O : the Odonaspidini.)

In scheme (a) the putative ancestor of the Parlatoriini gave rise to the Rugaspidiotini, and the Odonaspidini evolved from the Rugaspidiotini ; the Parlatoriini have no immediate relation with the Rugaspidiotini and the Odonaspidini.   In scheme (b) the Rugaspidiotini evolved from the ancestor of the Parlatoriini as in scheme (a), whereas the Odonaspidini have their origin in the Parlatoriini ; the Rugaspidiotini and the Odonaspidini are not immediately related.

The other side of the coin

The genus *Smilacicola*, here representing the Rugaspidiotini and including the three known species, is polymorphic in the second instar, and the polymorphic forms are interpreted as representing the character patterns of ancestral forms which belonged to different evolutionary times.   These patterns are discontinuous, and when one of them is manifested the other patterns should be maintained as potential in the genome (Takagi 1983).

The Odonaspidini as a group are also polymorphic in the second instar male. So far as represented by some Asian species in hand parlatoriine-patterned forms prevail in this stage.   They are quite reminiscent of *Parlatoria*.   [In fact, *Parlatoria zeylanica*, described by Rutherford (1915 p. 13) as adult female, must be the second

instar male of an *Odonaspis* species (*O. secreta* or *O. greeni*)]. Although the polymorphism is to be interpreted on the basis of a comprehensive study throughout the tribe, the parlatoriine-patterned forms certainly point to the origin of the Odonaspidini as in the case of *Smilacicola*. When other forms are manifested, the parlatoriine pattern should only be suppressed and not lost.

"Cryptic maintenance of [ancestral] phenotypic potential can only be one side of the coin. Changes in regulatory schemes....can result in entirely new, large-scale phenotypic experiments." (Hunkapiller et al. 1982). When the same reasoning is applied to the odonaspidine second instar polymorphism as interpreted above, it may be assumed that, prior to the evolution of the Odonaspidini, the odonaspidine pattern of characters was ready as potential in the genome of the form ancestral to the Parlatoriini [when scheme (a) is adopted] or of the Parlatoriini [scheme (b)]. If persistence of a taxon is based on persistence of the regulatory scheme of the genome, the existing Parlatoriini may still maintain the odonaspidine phenotypic potential.

The two newly described scale insects, *Neparla katus* and *Tamilparla smilacis*, relate well with this problem. They undoubtedly belong to the Parlatoriini and appear to be closely related to *Parlatoria*. The characters mentioned in distinguishing them from *Parlatoria* except character (2) of *Tamilparla* all agree or approach the state which exists in the Odonaspidini. Further, character (2) of *Tamilparla* may be related to the marginal scleroses occurring in the Odonaspidini. The two parlatoriines also agree with the Odonaspidini in their living under part of the plant body : they were found beneath the stipule of the host plant, and the Odonaspidini occur under the leaf sheath of bambusaceous or gramineous plants. The species of *Smilacicola* also live under the stipule of the host plant (*Smilax*) or (probably secondarily) in fungal mass. (Most of the North American species referred by Ferris (1938) to *Rugaspidiotus* were reported to occur in cracks in the bark.) So far as I am aware, such a cryptic mode of life is foreign to other parlatoriines.

Living in a depressed space under the stipule or the leaf sheath and the bivalve-type exuviation of the second instar female are common to all of *Neparla, Tamilparla*, the Odonaspidini, and *Smilacicola*. This combination of life mode and exuviation type appears to be peculiar to these taxa ; to my knowledge, in other groups of the Diaspididae (Aspidiotini ; Lepidosaphedini ; Diaspidini) species occurring at such cryptic sites exuviate in the way usual with the family (that is, their exuviation is not of the bivalve type). The second female exuvial casts of odonaspidines often show irregularly split margins of the dorsal and ventral halves (Fig. 7), suggesting that they were torn by force from the inside. This is apparently associated with the thickening of the cast on the ventral as well as dorsal surface.

It seems that change of habitat (under the stipule or the leaf sheath) followed by thickening of the second female exuvial cast was the primary cue toward the manifestation of odonaspidine characters. In *Neparla katus* and *Tamilparla smilacis*, however, the manifestation of further odonaspidine characters is not uniform between these species and among characters. In *Neparla* the arrangement of the perivulvar disk pores is the same as in odonaspidines ; macroducts occur on the ventral surface of the pygidium, too, as in the Odonaspidini, but are confined on this surface to a narrow marginal to submarginal area, and the pygidial macroducts on both surfaces show no trace of size reduction ; the plates are rudimentary outside

the third lobes, yet well represented between the lobes. In *Tamilparla* the perivulvar disk pores are arranged in five groups as usual with diaspidids; macroducts are somewhat reduced in size and, as in the Odonaspidini, strewn over the dorsal surface of the pygidium, but do not occur on the ventral surface; the plates as well as the lobes show no trace of reduction. In the first stage both species are little different from *Parlatoria* as represented by the nominifer *P. proteus*.

These two species show that odonaspidine characters can evolve in the Parlatoriini. The characters manifested include the arch-forming arrangement of the perivulvar disk pores, which is the only observed arrangement in the Odonaspidini and has not been found in the Rugaspidiotini (if *Natalaspis* is a rugaspidiotine). All this supports scheme (b) in the foregoing section as the more probable, thus suggesting that the Rugaspidiotini and the Odonaspidini have independent origins in spite of their agreement in general body structure.

In the foregoing discussion three postulations are set forth. First, character patterns should be ready as potential prior to their emergence; a new pattern should be prepared long in advance. Secondly, ancestral phenotypic potential should be maintained; character patterns of ancestors which appeared at different evolutionary times may not be lost. Lastly, some external factor should act as a trigger for the manifestation of a new pattern; change in life mode can be the trigger.

These postulations are based on taxonomic observations. I think that they are harmonious with recent structuralist or organizational interpretations of evolution (e.g. Webster and Goodwin 1982, Campbell 1985, Kauffman 1985). Preformation is advocated by Lima-de-Faria (1983) as a general principle in biology. Maintenance of ancestral phenotypic potential is required by studies in experimental morphology (e.g. Hampé 1959, Kollar et al. 1980) and paleontology (e.g. Smith 1975), too. Britten and Davidson's (1969) model for gene regulation has not been rejected and may be adopted for explaining the capacity of the genome to maintain phenotypic potential. Campbell (1985) advances "sensory evolution" and claims that "an organism detects relevant information about its environs and influences the way that it evolves accordingly."

Parallel evolution

One of the inevitable consequences of the postulations stated above is abounding occurrence of parallel evolution. The current interpretation of the bird and *Archaeopteryx* digits requires that the feather and its *complex* structure should have evolved independently at least twice (Hinchliffe et al. 1984) [unless it was completed by the common ancestor of the existing birds and *Archaeopteryx*]. It is well known that many reptiles belonging to different orders provide intrauterine nourishment to their young and bear live young. In the foregoing discussion the Rugaspidiotini and the Odonaspidini are supposed to have derived from the putative ancestor of the Parlatoriini and the Parlatoriini, respectively. The characters common to both tribes should have evolved independently. Parallel evolution of odonaspidine characters is also probable among different lineages originating from the Parlatoriini, because *Neparla katus* and *Tamilparla smilacis* apparently cannot be connected within the same and single evolutionary lineage. The possibility, then, cannot be ruled out that the existing Odonaspidini are polyphyletic, being composed of parallel lineages. They agree in their host plants (Bambusaceae or Gramineae) and, so far

10

as known, are fairly uniform in the antennal characters of the first instar. But this alone cannot be sufficient evidence against the possibility of their polyphyletic origin, because these agreements might also be due to parallel evolution. Complete parallel evolution if occurring will result in a group of species which cannot expect but to be interpreted as monophyletic by seemingly autapomorphic characters. (I do not necessarily refuse to accept a polyphyletic group as a taxon unless it proves to be formed by convergence. This problem of taxonomy is, however, beyond the scope of this paper.)

Whereas atavistic phenotypes can literally be abrupt when they appear (Takagi 1983), evolutionary changes must in principle be gradual, because any change should fulfill an internally consistent programme of development. Manifestation of phenotypic potential which has not been manifested previously in the evolutionary lineage concerned must, therefore, be a process adjusted by trial and error. As suggested by *Neparla katus* and *Tamilparla smilacis*, the manifestation of odonaspidine characters in the evolution of the Odonaspidini might have proceeded gradually and, if it occurred in different lineages, not uniformly. In this case, initial genetic differences might have produced different effects on the manifestation according to the lineages. Further, random mutation, genetic drift and selection might have inserted accidental modifications in the course of gradual manifestation of odonaspidine characters. The occurrence of complete parallel evolution, therefore, appears less probable. On the other hand, parallel evolution may be complicated and obscured by diversification of forms through speciation.

I have examined larvae of some odonaspidine species. A certain species from Malaya shows unusual features in the first and second instar males. The North American *Odonaspis minima* is peculiar in the second instar male (Howell et al. 1978). Detailed study of the larval stage in Asian, African and American species of the Odonaspidini and the Rugaspidiotini is, therefore, necessary in order to proceed with the problem of the origin and evolution of these groups.

In conclusion, new forms appear basically as the manifestation of potential held in the order present in the preceding form. This process is literally 'evolution', unrolling of something ready. Mutation and selection are, then, to be studied in terms of their roles in the manifestation and their interrelations with the order.

REFERENCES

Britten, R.J. & Davidson, E.H. 1969. Gene regulation for higher cells: a theory. Science 165: 349-357.
Campbell, J.H. 1985. An organizational interpretation of evolution. In: Depew, D.J. & Weber, B.H. (eds.), Evolution at a crossroads, The MIT Press, Cambridge, Mass., pp. 133-167.
Ferris, G.F. 1938. Altas of the scale insects of North America 2.
Hampé, A. 1959. Contribution a l'étude du développement et de la régulation des déficiences et des excédents dans la patte de l'embryon de poulet. Archives d'Anatomie Microscopique et de Morphologie Expérimentale 48: 345-478.
Hinchliffe, J.R. & Hecht, M.K. 1984. Homology of the bird wing skeleton. Embryological versus paleontological evidence. Evolutionary Biology 18: 21-39.
Howell, J.O. & Tippins, H.H. 1978. Morphology and systematics of *Odonaspis minima* n. sp. Annals of the Entomological Society of America 71: 762-766.

Howell, J.O., Beshear, R.J. & Tippins, H.H. 1986. Descriptions of first instars of type-species of the nominal genera of three subtribes of the Diaspidini. J. Entomol. Sci. 21 : 1-9.

Hunkapiller, T., Huang, H., Hood, L. & Campbell, J.H. 1982. The impact of modern genetics on evolutionary theory. In : Milkman, R. (ed.), Perspectives of evolution, Sinauer Ass., Mass., pp. 164-189.

Kauffman, S.A. 1985. Self-organization, selective adaptation, and its limits : A new pattern of inference in evolution and development. In : Depew, D.J. & Weber, B.H. (eds.), *Evolution at a crossroads*, The MIT Press, Mass., pp. 169-207.

Kollar, E.J. & Fisher, C. 1980. Tooth induction in chick epithelium : expression of quiescent genes for enamel synthesis. Science 207 : 993-995.

Lima-de-Faria, A. 1983. Molecular evolution and organization of the chromosome. Elsevier, xliv+1186 pp. ["Principle of preformation", pp. 1078-1079.]

Mamet, R. 1959. Notes on the Coccoidea of Madagascar IV. Memoires de l'Institut Scientifique de Madagascar E 11 : 369-479.

Rutherford, A. 1915. Some new Ceylon Coccidae. Journal of the Bombay Natural History Society 24 : 111-118.

Smith, G.R. 1975. Fishes of the Pliocene Glenns Ferry formation, Southwest Idaho. University of Michigan Museum of Paleontology, Papers on Paleontology 14, 68 pp.

Takagi, S. 1983. The scale insect genus *Smilacicola*, with particular reference to atavistic polymorphism in the second instar (Homoptera : Coccoidea : Diaspididae). Insecta Matsumurana New Series 27 : 1-36.

Webster, G. & Goodwin, B.C. 1982. The origin of species : a structuralist approach. Journal of Social and Biological Structures 5 : 15-47.

Fig. 1. *Neparla katus*, adult female : body, antenna, macroducts on mesothorax, and "crack" of derm on metathorax. Godavari. Scale : 0.1 mm for body ; 0.01 mm for parts outside.
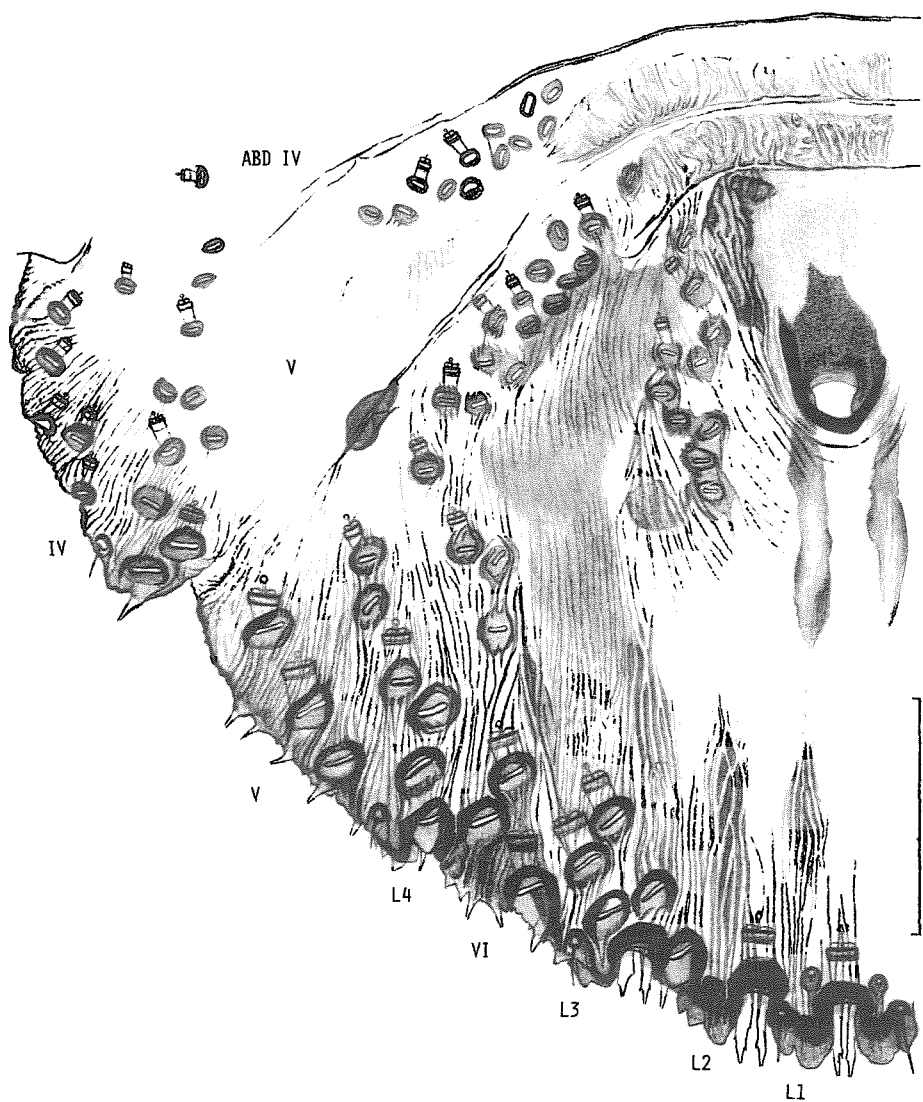
Fig. 2. *Neparla katus*, adult female : pygidium, dorsal surface. Godavari. Scale : 0.05 mm.

Fig. 3. *Neparla katus*, adult female : pygidium, ventral surface. Godavari. Scale : 0.05 mm.

Fig. 4. *Neparla katus*, 2nd instar female : body and pygidial margin, dorsal surface. Godavari. Scale : 0.1 mm for body ; 0.05 mm for pygidial margin.
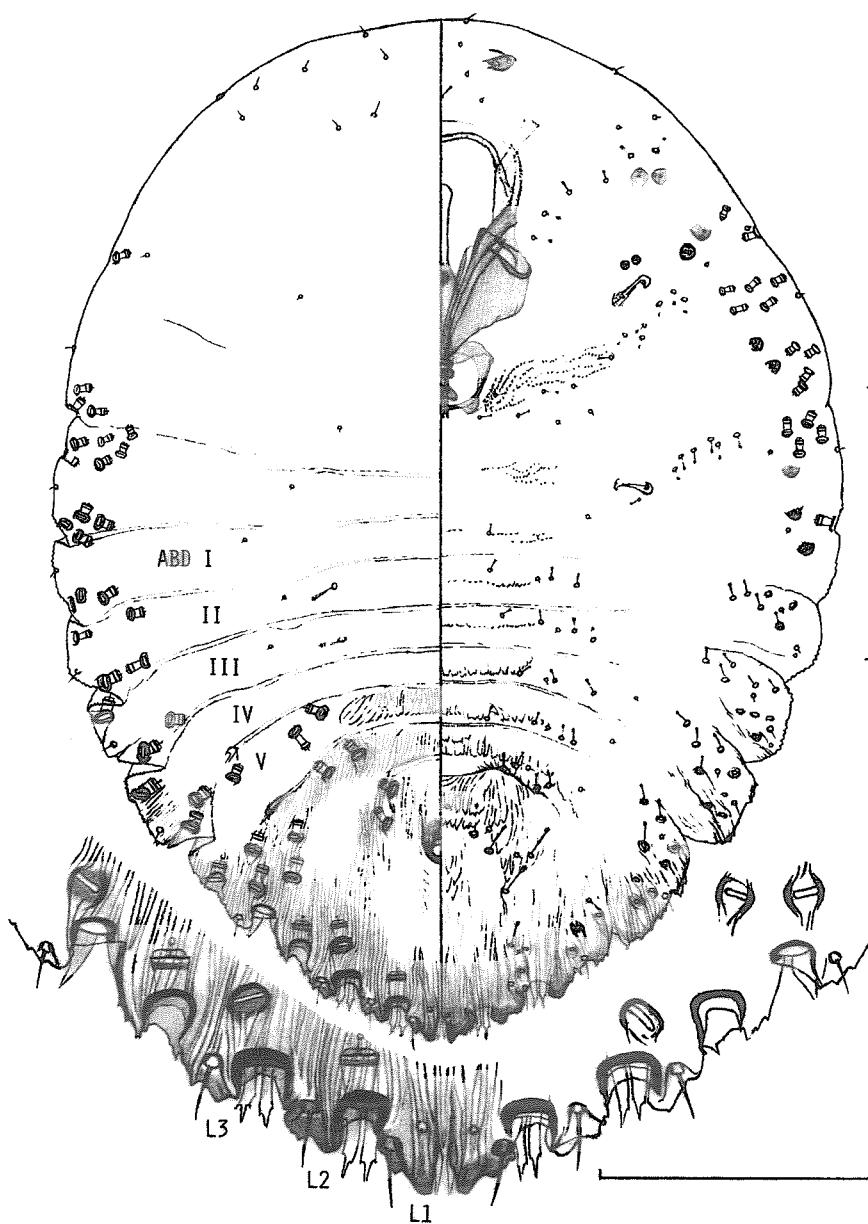
Fig. 5. *Neparla katus*, 2nd instar male : body and pygidial margin, dorsal surface.
Godavari. Scale : 0.1 mm for body ; 0.05 mm for pygidial margin.
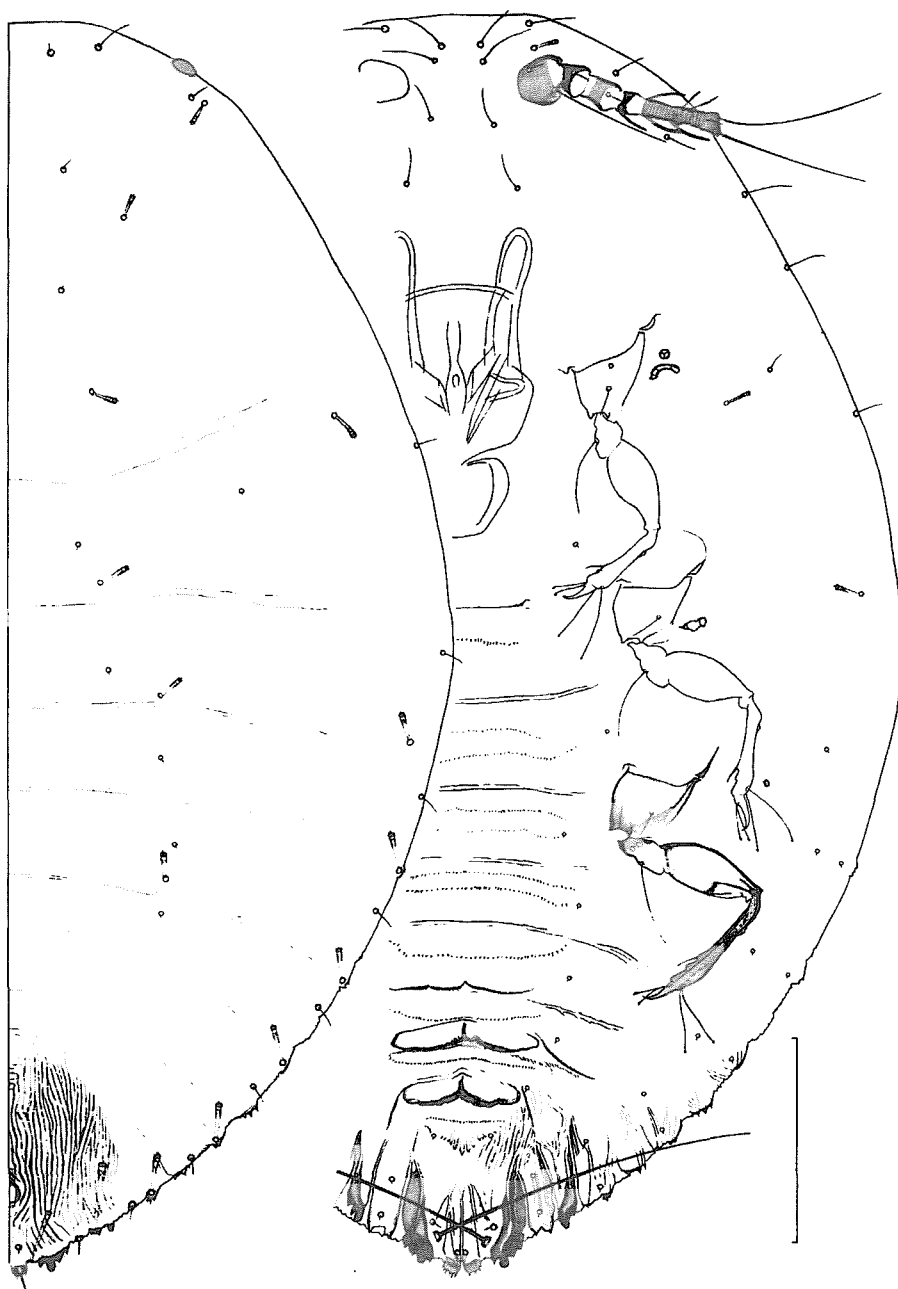
Fig. 6. *Neparla katus*, 1st instar male. Phidim. Scale : 0.05 mm.
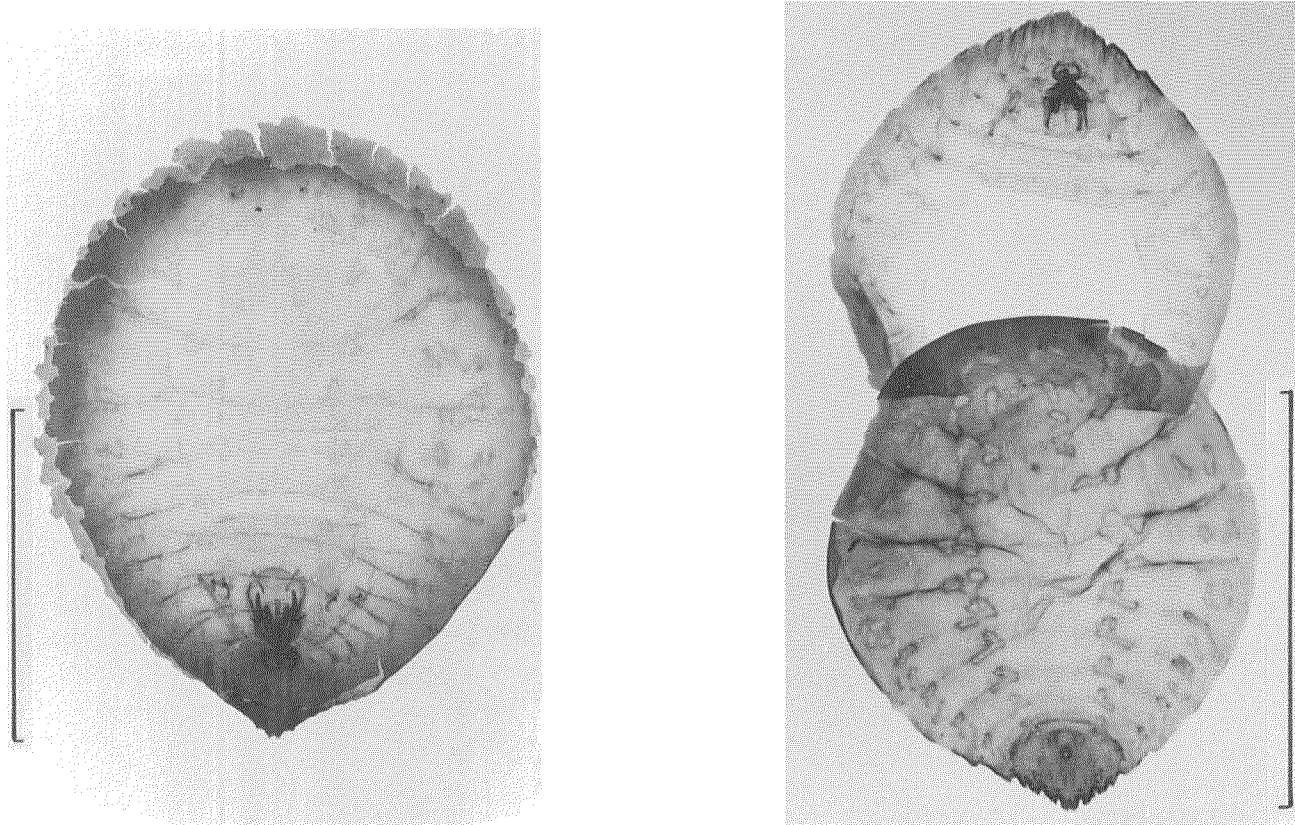
Fig. 7. Right. *Neparla katus*, exuvial cast of 2nd instar female. Phidim. Scale : 0.5 mm. Left. *Odonaspis greeni*, exuvial cast of 2nd instar female. Japan, on *Miscanthus*. Scale : 0.5 mm.
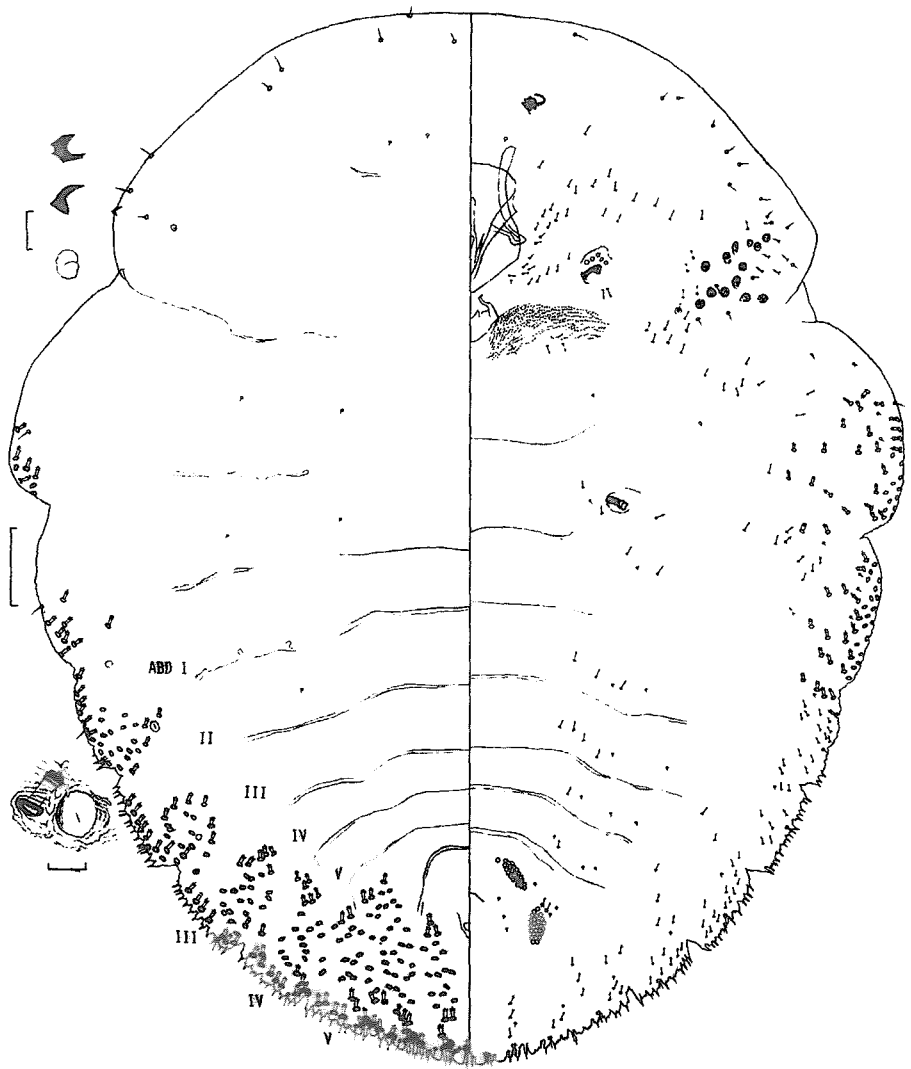
Fig. 8. *Tamilparla smilacis*, adult female : body, modified eyes, and membranous "bosses" on prothorax and abdomen. Scale : 0.1 mm for body ; 0.01 mm for parts outside.
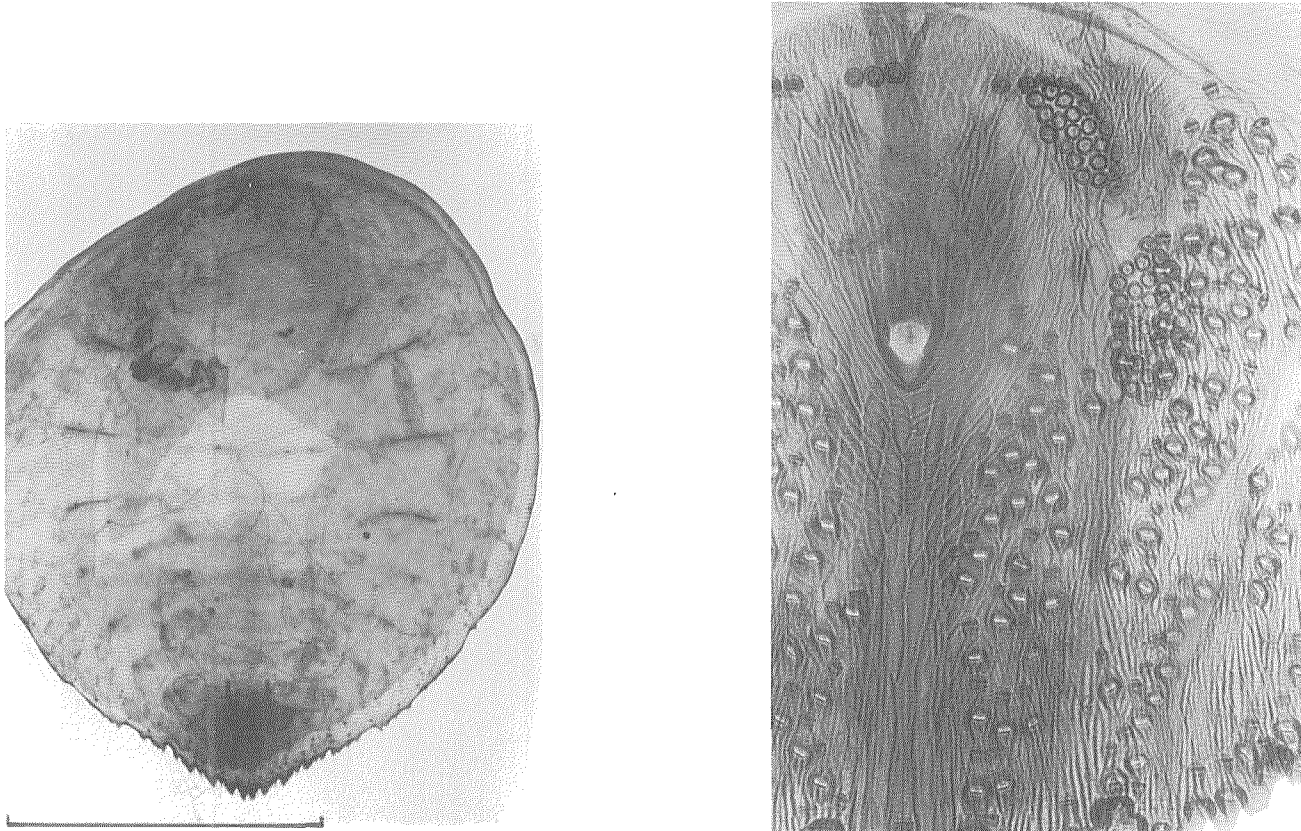
Fig. 9. *Tamilparla smilacis*, adult female : pygidium.

Fig. 10. Right. *Tamilparla smilacis*, adult female: part of pygidium showing reticulation of derm around anus. Left. *Tamilparla smilacis*, exuvial cast of 2nd instar female. Scale: 0.05 mm.
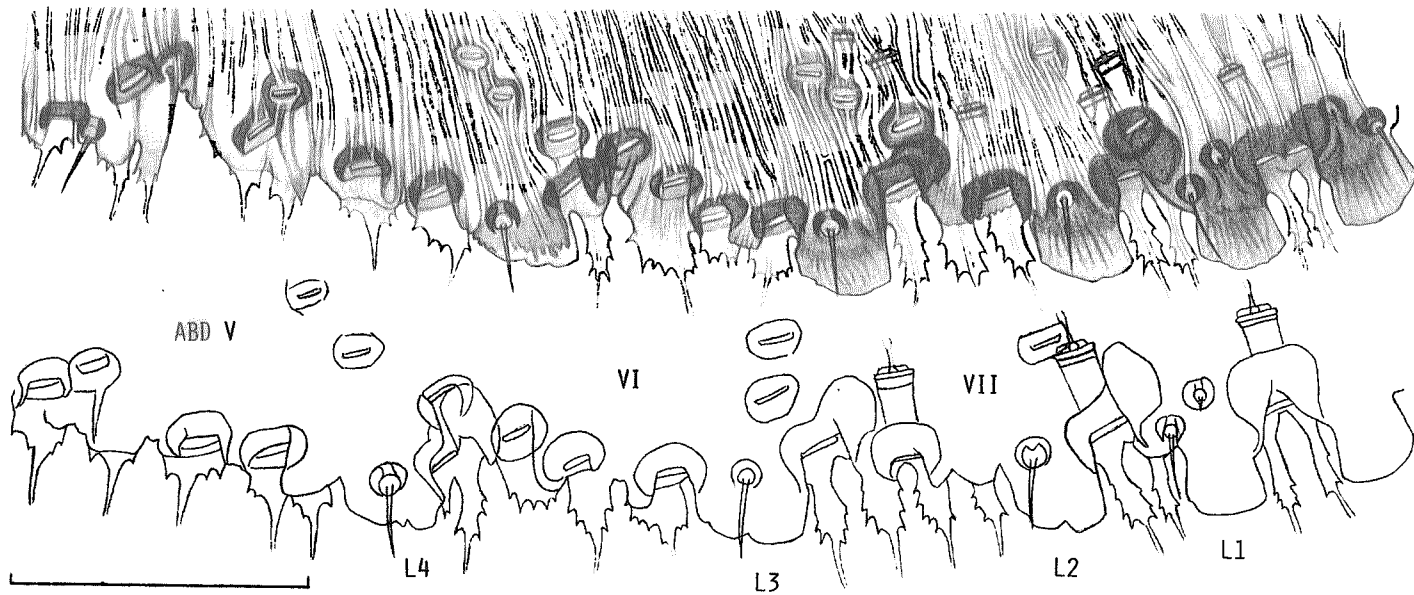
ABD V

VI

VII

L4

L3

L2

L1

Fig. 11. *Tamilparla smilacis*, adult female : pygidial margins, dorsal surface. Scale : 0.05 mm.
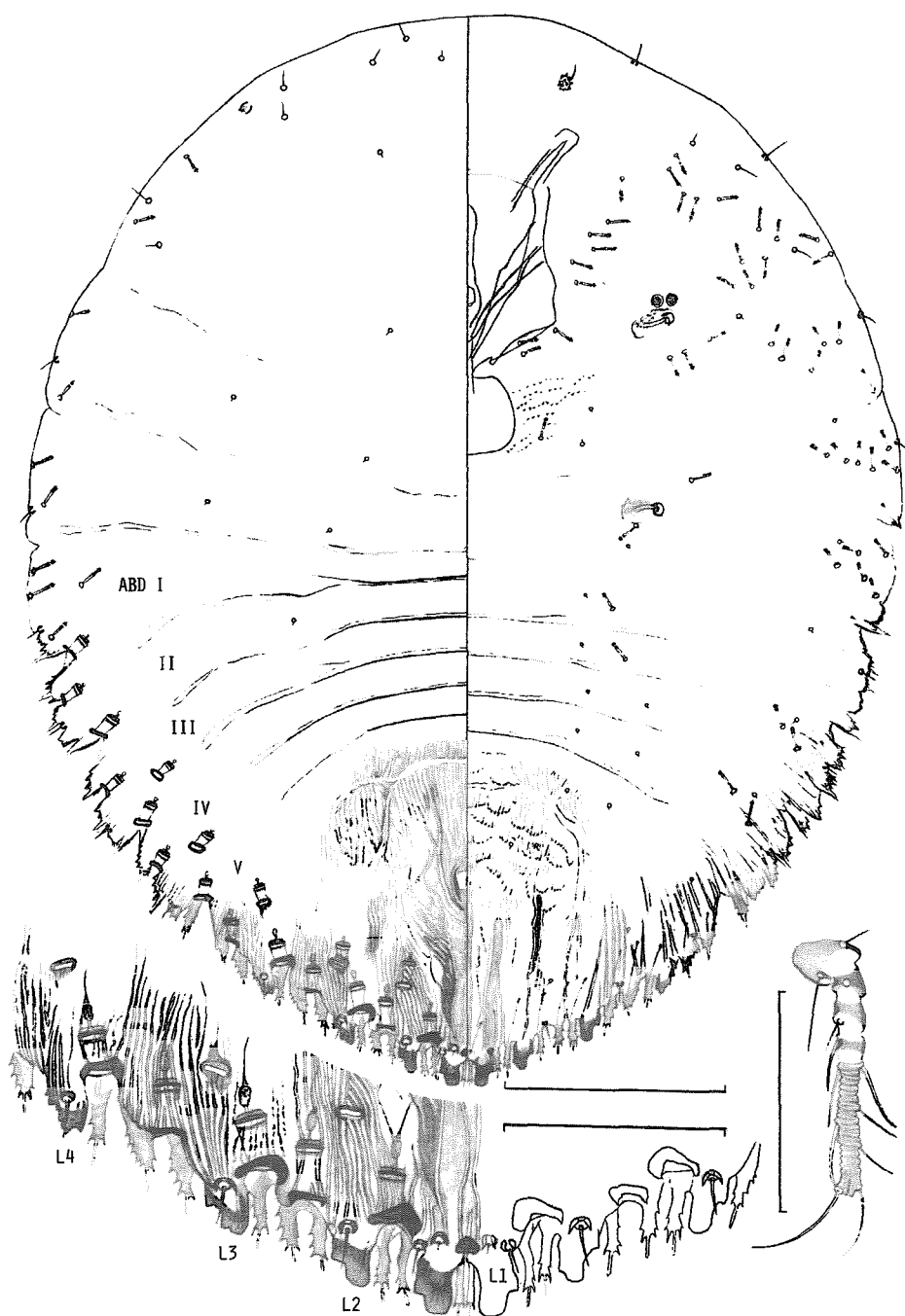
Fig. 12. *Tamilparla smilacis*, 2nd instar female: body and pygidial margin, dorsal surface. Scale: 0.1 mm for body; 0.05 mm for pygidial margin. Right below. *Tamilparla smilacis*, 1st instar: antenna. Scale: 0.05 mm.
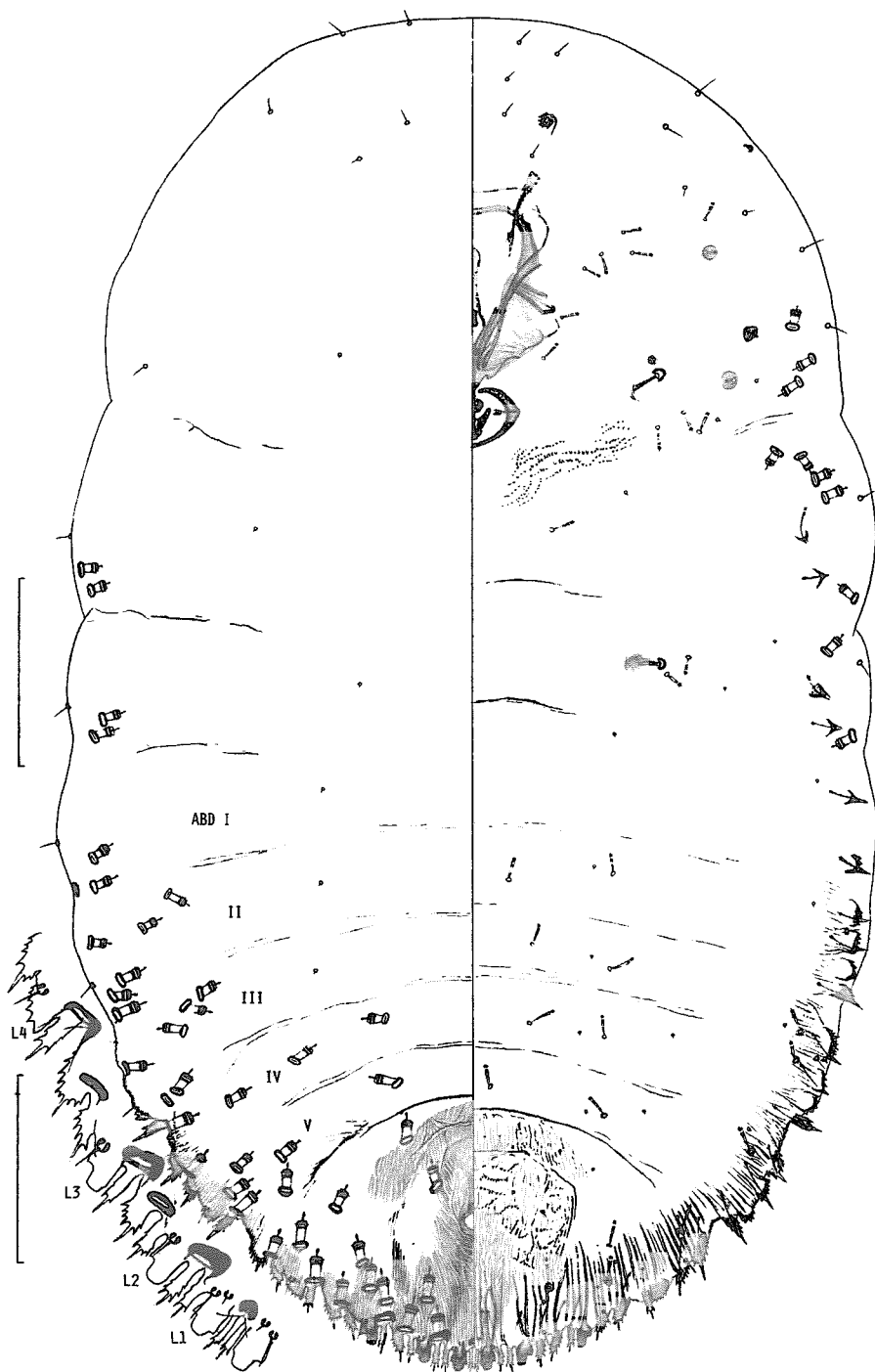
Fig. 13.　*Tamilparla smilacis*, 2nd instar male : body and pygidial margin, dorsal surface.
　　Scale : 0.1 mm for body ; 0.05 mm for pygidial margin.